

Brood Relief Behaviour of the Cichlid Fish *Etroplus maculatus*

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Brood Relief Behaviour of the Cichlid Fish *Etiloplus maculatus*

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With 14 figures

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Abstract

Quantitative recordings were made of the behaviour of *Etiloplus maculatus* parents caring for eggs and wrigglers. Spatial and temporal aspects of brood relief behaviour are examined in connection with parent size, time of day, interval since spawning and the frequencies of occurrence of other behaviours. Functional aspects of Cichlid brood relief behaviour are discussed and compared with those of avian nest relief.

Introduction

In many substrate-brooding Cichlid fish, including *Etiloplus maculatus*, parents relieve each other at brood care tasks. While one stays close to the eggs or wrigglers, fanning and cleaning them, the other patrols and defends the territory; at intervals the patrolling parent approaches the brood and the mates switch tasks. Most monogamous Cichlids organize brood care activities in this way, although the proportions in which male and female parents divide the tasks may vary from species to species.

There is a striking similarity between Cichlid brood relief and nest relief where it occurs in birds (LORENZ 1935, p. 344). Cichlids resemble birds even in their apparent reluctance to cede the position close to the brood, and in the ritualized nature of the mates' interactions prior to switching. The term 'relief ceremonies' is used by students of fish behaviour and ornithologists alike.

However, Cichlid brood relief differs radically from bird nest relief in the little attention it has received. The study of avian incubation is practically a science in itself, and an abundance of data on nest relief schedules of various species has been published (e.g. DRENT 1975; SKUTCH 1962). Yet for Cichlid brood relief, although it has been described quite frequently (e.g. BAERENDS and BAERENDS-VAN ROON 1950, p. 161; BAYLIS 1974; COLE and

WARD 1969; LAMPRECHT 1973; SMITH-GRAYTON and KEENLEYSIDE 1978), there are hardly any quantitative studies of switching schedules (but see OHM 1958/59), and speculations on its functional significance are practically non-existent.

Cichlid brood relief is remarkable for its high degree of interdependence in the behaviour of male and female parents. Knowing what one parent is doing at any given time appreciably narrows the range of probable simultaneous behaviours of its mate. The following report examines form and extent of this coordination from a laboratory study on the brood relief behaviour of *Etoplus maculatus*. The parents' spatial positions relative to the brood and each other offer a convenient way of representing switching behaviour. Spatial data are used in Section (1) to demonstrate the close coordination between mates, and in (2) to probe the rules of temporal organization of brood relief behaviour. (3) deals with the relationship of positional changes to brood care activities and other behaviours. On the basis of these results the Discussion (4) treats the possible mechanism and function of this precise coordination, and compares the situation in Cichlids to that in birds.

Etoplus maculatus and its Reproductive Behaviour

E. maculatus is a laboratory favourite of ethologists. There are studies on its behavioural ontogeny (e.g. WYMAN and WARD 1973), courtship behaviour (e.g. BARLOW 1970), parent-offspring communication (e.g. COLE and WARD 1970) and aggressive behaviour (e.g. REYER 1975). Field observations have been published by WARD and WYMAN (1975, 1977). More detailed field data on time budgeting are being prepared for publication by WARD, and by SAMARAKOON.

E. maculatus occurs in fresh or brackish inland lakes or coastal lagoons in Sri Lanka and S.E. India. In captivity it may reach a standard length of about 7.5 cm. Both sexes are yellow with a black lateral spot, ♀♀ having iridescent white bands on the upper and lower margins of the caudal fin.

WARD and WYMAN (1977) report that in the wild the species breeds in shallow water at a density of up to two pairs per m², the ♂ of a breeding pair usually being slightly larger than the ♀. The authors observed intra-specific predation on eggs and young, and extremely prolonged parental care continuing until the young were nearly as big as the parents — an unusual phenomenon in Cichlids.

In our laboratory the ♂ was not necessarily the larger member of a pair. A courtship period of two or more days preceded spawning. The ♀ deposited several hundred eggs in one layer on a hard even surface. Sheltered spawning sites were preferred. In the regular feeding and lighting conditions of the lab, pairs usually spawned in the early afternoon. Wrighlers emerged in the early morning of the third day after spawning and were carried by the parents to a previously prepared pit in the substrate. Four or five days after the transfer the young began to swim free. Brood relief behaviour occurred during the egg and wrighler care periods and during the first days of guarding the school of free-swimming fry (COLE and WARD 1969).

Material and Methods

Animals

E. maculatus were obtained several times during the program, from various sources. They had presumably all been bred in captivity for more than one generation. Individuals used in the experiments were 4.0 cm to 7.5 cm long (SL) and weighed 3.5 g to 18.5 g.

Maintenance

The tanks used had a volume of 400 l and were 53 cm high with a ground area of 128×60 cm. The bottom was covered with fine gravel. PVC boards, flower-pot halves and large stones provided hiding and spawning sites. The water was slightly brackish, with a pH value of about 8 (1 heaped teaspoon of salt added per 10 l, turf filter). The temperature lay between 27 °C and 29 °C. Full lights were on from 8.00 h until 21.00 h, preceded and followed by a 20 min twilight period. The fish were fed at noon with commercial dried food (TetraMin) or *Tubifex* worms.

Tank occupation

When not otherwise specified a breeding pair was alone in a tank.

In one set of 6 experiments non-breeding conspecifics were added as brood predators (WARD and WYMAN 1977). Such 'intruders' weighed about 5.0 g and were usually smaller than breeding individuals. During egg care successive batches of 3–12 intruders were released into an observation tank every few h on one day, and breeding pair behaviour under accumulating intruder pressure was observed. Groups of intruders staged collective raids on the eggs. No pair was able to defend the brood against more than 24 intruders.

Recording of observations

Observations were made mainly during egg, but also during wriggler care. An observation period lasted 1 h. The observer sat quietly about 2 m from the tank, visible to the fish. To check for observer disturbance the behaviour was monitored occasionally via a Video system. The behaviours of a mated ♂ and ♀ were recorded simultaneously on punched paper tape with a time resolution of 1 s (for details of the recording apparatus see FERNALD and HEINECKE 1974). The categories recorded are defined at appropriate places in the text [at the beginnings of (1), (2), (3)].

(1) Spatial Coordination of ♂ and ♀

Fanning and mouthing eggs or wrigglers require a parent's intimate closeness to the brood. These activities are performed by one parent at a time, who usually also stays intimately close to the brood between bouts of these behaviours. Meanwhile the mate moves about the tank at a distance from the brood. To distinguish the two modes of behaviour during observations a category 'Near Brood' was defined.

Near Brood (NB): The parent (whose eye is used as reference point in assessing distance) is within 15 cm of the brood.

The time spent Near Brood by the members of isolated pairs is examined in (a) below; (b) shows the effect of conspecific intruders on this time; in (c) a description of the parents' movements over the whole tank area is given, and (d) contains some comments on the results.

(a) Time spent by parents Near Brood, without intruders

Four situations were recognized: both parents Near Brood, the ♂ alone, the ♀ alone, neither parent Near Brood. The observed time spent by a pair in each of these four states per obs. period was compared with the time to be expected if each parent were moving independently of the other but spending just as long Near Brood (e.g. expected time ♂ alone NB = time ♂ NB $\times$ time ♀ not NB/total time).

Fig. 1 compares observed and expected values in each state for 30 obs. periods, two each on 15 pairs (30 individuals). The states 'both parents Near Brood' and 'neither parent Near Brood' were much less frequent than expected for independent movement; time spent Near Brood by ♂ or ♀ alone varied widely, but was always clearly more frequent than expected for independent movement.

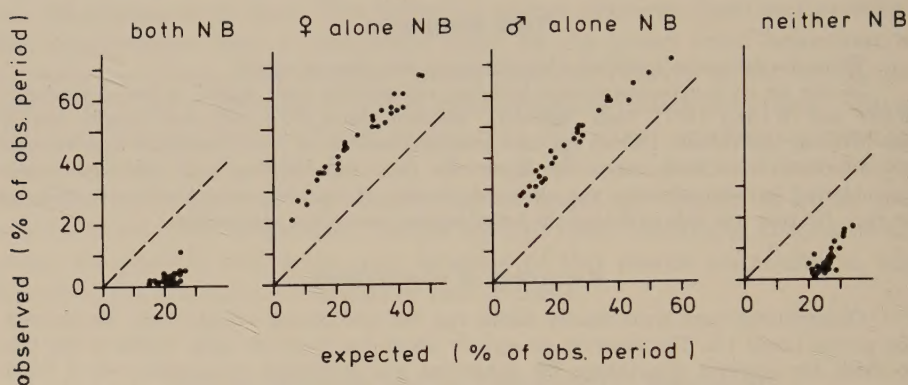


Fig. 1: Observed and expected times spent Near Brood (NB) in 30 obs. periods

(b) Time spent by parents Near Brood, with intruders

For six pairs, time spent Near Brood in the presence of zero, three and six conspecifics was recorded (three obs. periods per pair). For each pair Fig. 2 shows time spent Near Brood by the ♀ alone, both parents, and the ♂ alone in the three situations. With three or six intruders, brood defence accounted for 3%—16% of the observation time.

As shown in Fig. 2, with increased threat to the brood the total time Near Brood decreases. In all pairs parents still spend less time simultaneously Near the Brood than if moving independently of each other. However, the

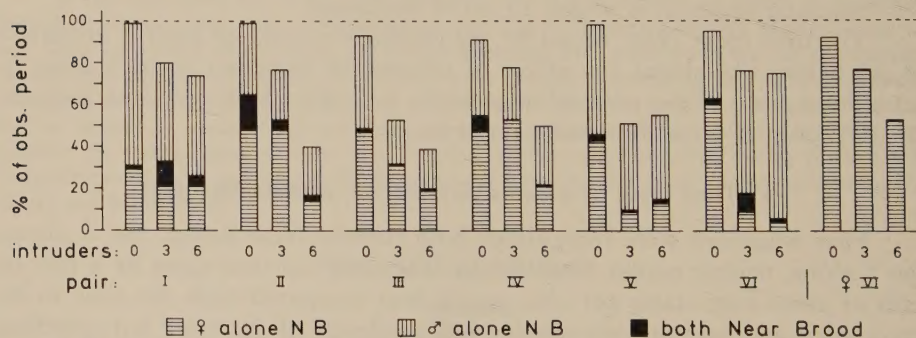


Fig. 2: Time spent Near Brood during egg care by members of 6 pairs (numbers apply to this Fig. only) and by a lone ♀ (see text) in obs. periods with zero, 3 and 6 intruders

time an individual parent stays Near Brood may even increase with mounting intruder pressure, as in the case of the ♂ of Pair VI, where the ♀ performs the bulk of brood defence.

Whether ♂ or ♀, a parent bereft of a mate invariably continued to care for the brood, staying Near Brood constantly save for very brief bouts of feeding, digging and brood defence (10 cases recorded, in which the brood was one day old or more). An example is given in the last three columns of Fig. 2, showing time spent Near the Brood by the ♀ of Pair VI during a breeding cycle in which her mate was removed after spawning. She spent nearly as much time Near the Brood as both parents together had previously done. Although as intruder pressure accumulated she too devoted more time to brood defence, her time spent Near the Brood was nevertheless still more than twice what it had been during shared brood care.

(c) Parents' movements over the whole tank area

Location data were recorded in a 300 l tank subdivided along its length into a row of 8 identical compartments each having 12×40 cm ground area. The dividers were only partial, so that the fish could pass freely in front and behind them, but the brood in one compartment was out of view of an animal in the next. A breeding pair was observed with 5–10 considerably smaller conspecifics, which drew attacks consuming only a few % of the pair's time. The locations of the ♂ and of the ♀ were noted simultaneously at 10 s intervals over several 20 min periods for each of three stages of the reproductive cycle: courtship (data on 2 pairs), egg care (data on 2 pairs) and wriggler care (data on 1 pair).

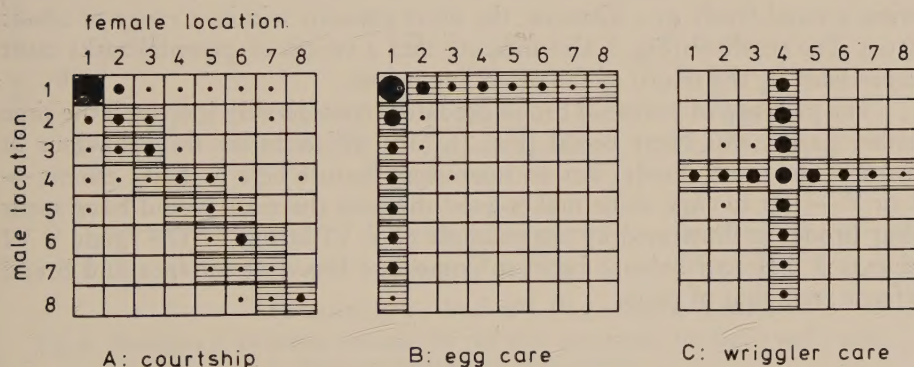


Fig. 3: Location matrices for 3 reproductive stages. Black disc area represents relative combination frequencies. Shaded cells: combination more frequent than if mates had moved independently (Cell 1—1 shaded in Matrix A, not in B)

Results are plotted in matrices in Fig. 3, columns giving female and rows male locations, so that a combination of two simultaneously observed locations defines each cell. Black disc size represents the relative frequency of a com-

ination. Shaded cells indicate a more frequent combination than could be expected if the mates had moved independently of each other, but had shown the same individual compartment preferences.

Cells near and on the descending diagonal in Matrix A are occupied: the mates are moving about the tank together. The future spawning site (Compartment 1) is already a preferred location. The mates' behaviour is closely interdependent, but in a completely different fashion than during brood care.

In Matrix B eggs are being cared for in Compartment 1. Cells of Row 1 and Column 1 are occupied pre-eminently: one or other parent is always in Compartment 1. A parent away from the brood may visit all compartments, but spends more time in those closer to Compartment 1. The parents spend a relatively long time *together* in Compartment 1, but less than if moving independently of each other.

In Matrix C, behaviour during wriggler care (wrigglers in Compartment 4) exhibits essentially the same characteristics.

(d) Remarks

In the undivided tank without intruders (1a) pairs spent median amounts of 2 % of their total time with both parents Near Brood and 5 % with neither parent Near Brood (Fig. 1). In the subdivided tanks (1c) parents were in the brood compartment simultaneously well over 10 % of the time, and outside it simultaneously less than 1 % of the time (Fig. 3). Are these results compatible?

In the subdivided tank a parent in the same compartment as the brood could be up to 30 cm from it, well out of Near Brood range as defined. If the results shown in Fig. 3 are representative, this means that even when neither parent is Near Brood, most of the time only one actually absents itself and swims around freely at a distance; the other remains within a range of about 30 cm. The results in Fig. 3 also indicate that a switch of parental tasks must be preceded by the return of the patrolling parent.

The presence of potential brood predators considerably increased the time neither parent was Near Brood (Fig. 2). (3d) will examine the behaviour in this situation more closely. But an interesting feature here is that a parent — ♂ or ♀ — left to cope alone makes good the time the mate would have spent Near Brood, as illustrated by the example of ♀ VI in Fig. 2. The single ♀ VI achieves a different balance between immediate brood attendance and brood defence from that of pairs.

(2) The Temporal Organization of Brood Relief

By a rough approximation brood relief behaviour can be described as an alternation between two states of a pair, one with the ♀ and one with the ♂ closer to the brood. Although this concept disregards the fact that the process of exchanging tasks is not a momentary affair, it provides a simple and useful representation of switching schedules.

Proximate and Remote Positions: The parent closer to the brood at any time is in the Proximate Position, its mate is in the Remote Position. There are thus two possible states of a pair: ♀ Proximate (♂ Remote) and ♂ Proximate (♀ Remote). An interval between switches is a 'turn'. A Proximate turn of one parent is the same length as the simultaneous Remote turn of its mate. This measure is completely independent of the definition 'Near Brood'. Even when the parents are both inside (or outside) the 15 cm radius, one is Proximate and the other Remote.

The following Section (a) uses Proximate and Remote Positions to describe switching schedules and (b) examines the distributions of turn lengths. (c) and (d) treat inter-pair and intra-pair variations in switching schedules. (e) shows the effect of intruders on switching schedules, and in (f) some comments are brought forward.

(a) Examples of switching schedules

Fig. 4 gives examples of switching schedules for two pairs. Each step function represents one obs. period. Data were collected at three different times during the egg care period.

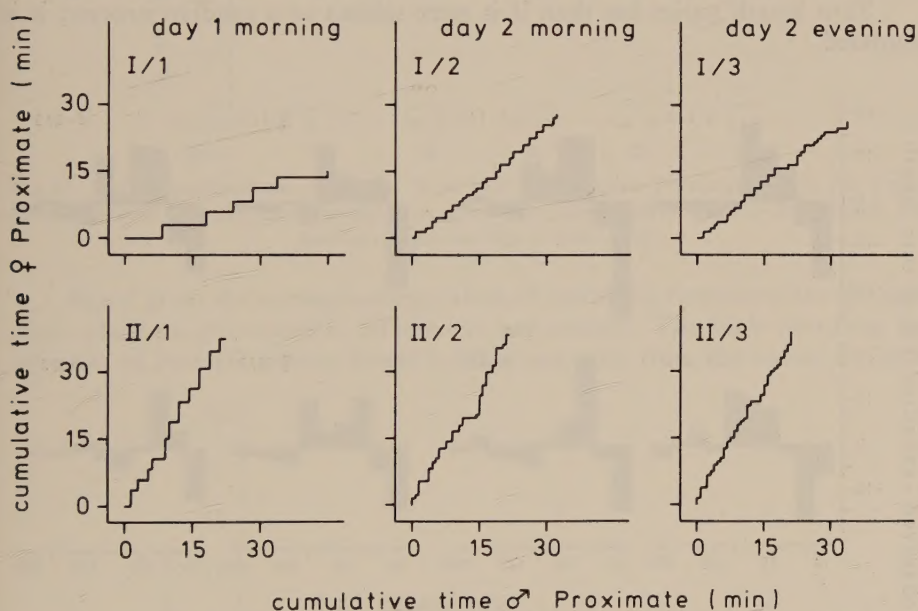


Fig. 4: Examples of switching schedules for two pairs (nos. apply for Figs. 4 and 5 only).
Each step function = 1 obs. period

Most turns last about 1–2 min. The switching schedules are very predictable on a short-term basis but vary greatly between pairs and over longer periods, either in the relative apportionment of tasks to ♂ and ♀ (the slope of the function) or in switching frequency (steps per time unit). Task apportionment and switching frequency define mean lengths of Proximate turns for ♂ and ♀.

(b) The distribution of turn lengths

Do turn lengths vary randomly or are they regular? To decide this question, observed distributions of turn lengths were compared with random distributions having the same mean.

Expected random distributions of turn lengths were computed as follows. Due to recording constraints no more than one switch could be recorded per s. Therefore the probability that a switch will occur during any given observation s can be directly deduced from f, the switching frequency per min, as $P_s = f/60$. The relative frequency r with which a turn of n s length should be expected to occur is then:

$$r = P_s (1 - P_s)^{n-1}.$$

Observed and expected turn lengths were compared in each obs. period by subtracting the expected from the observed distribution of turn lengths. For those switching schedules from Fig. 4 with relatively many steps the resulting difference distributions for ♂ and ♀ turns are plotted in Fig. 5. In all cases the difference value is positive only towards the centre of the distribution: turns with length deviating far from the mean in either direction occurred less frequently, turn lengths close to the mean more frequently than expected.

Turn length varies less than if it were subject to a random process; it is regulated.

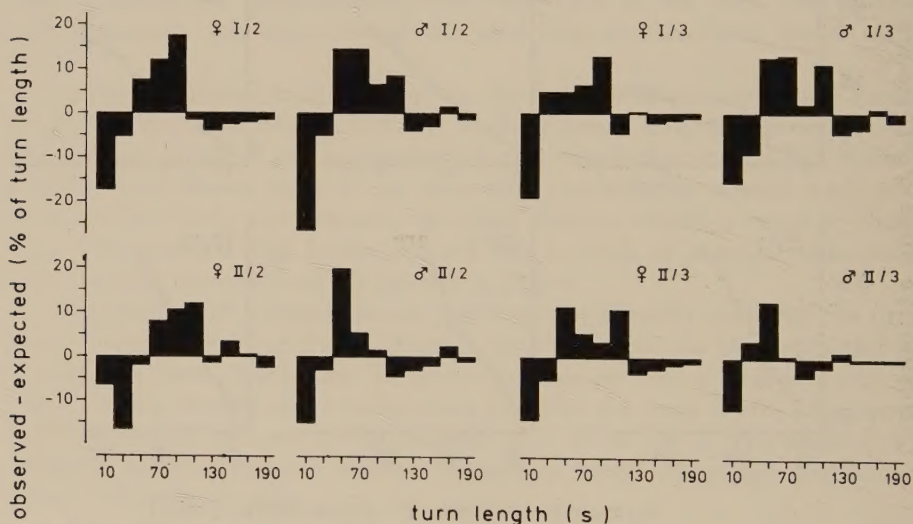


Fig. 5: Observed and expected difference distributions for male and female turn lengths for 4 of the switching schedules in Fig. 4 (Pairs I, II, protocol nos. 2, 3). Distributions truncated on right

(c) Inter-pair differences in switching schedules

Switching schedules vary in both task apportionment and switching frequency, as for example in Fig. 4. To what extent could this be due to inter-pair variation?

For five pairs (10 individuals) extensive data on switching schedules were collected over more than one breeding cycle. Obs. periods were distributed as evenly as possible over the first and second days after spawning. Fig. 6 gives the resulting task apportionment values per obs. period. It is apparent that part of the variation in task apportionment can be attributed to inter-pair differences. If each pair is assessed as belonging to one of three task apportionment types — ♂ Proximate longer, ♀ Proximate longer, ♂ and ♀ equal — we see that a pair remains true to its type throughout consecutive broods.

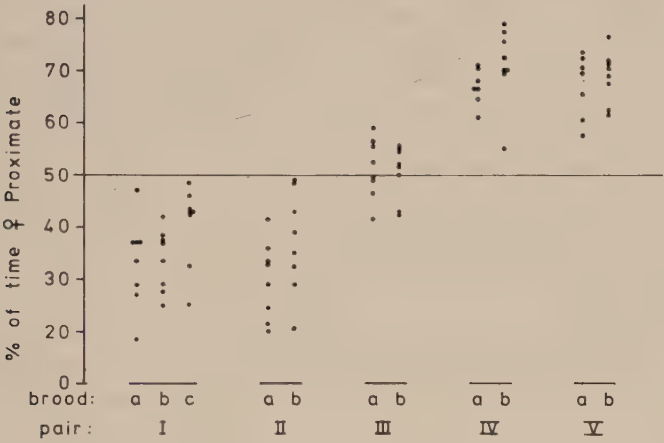


Fig. 6: Task apportionment values (in % of obs. period spent Proximate by ♀) for 5 pairs (2 or 3 broods per pair) during egg care. Each data point represents one obs. period. Pair numbers apply for Figs. 6 and 7 only

Fig. 7 gives the corresponding values of switching frequency for the same data. Here no pair-specific differences are evident. The high switching frequencies of Pair III during Brood b differ not only from the values for other

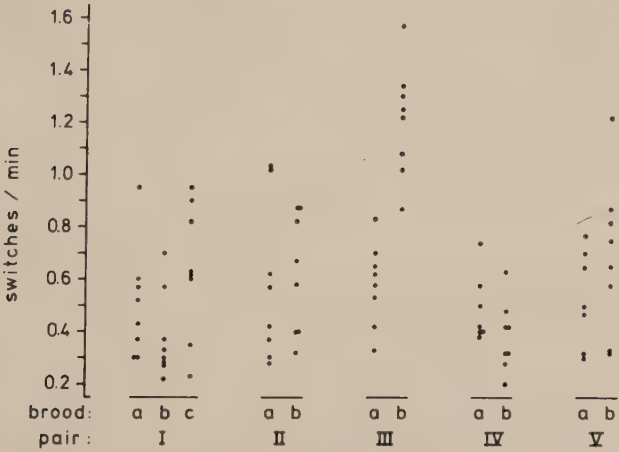


Fig. 7: Switching frequency values for data used in Fig. 6

pairs but also from their own during Brood a. Such consistently high switching frequencies were not observed again in any pair, and their cause in this case is unknown. But despite this difference in switching frequencies between breeding cycles IIIa and IIIb, task apportionment (Fig. 6) remained true to type.

What characteristics determine a pair's typical task apportionment? One noticeable difference between the experimental pairs was in the relative size of the mates. For 18 pairs (36 individuals), each observed during egg care for 2–24 obs. periods (some pairs over several broods), the relative weight of ♀ to ♂ was correlated with median task apportionment (% of time ♀ Proximate). A positive correlation significant at $p < .01$ was found (Kendall rank correlation, $\tau = .46$): the larger parent tends to spend more time in the Proximate Position than its mate. Curiously, from the same data, the larger parent was not found to spend significantly more time Near Brood than its mate. This difference is in part because the smaller mate spent more of its Remote time within the 15 cm (Near Brood) area: the relative weight of ♀ to ♂ was positively correlated with the ♀ : ♂ ratio of their time spent Near Brood while Remote ($p < .01$, Kendall rank test, $\tau = .48$).

No connections were found between task apportionment and any individual or pair characteristics other than size. Moreover, the correlation between task apportionment and relative mate size holds good only for undisturbed pairs. Task apportionment may change radically when a pair is defending its brood (2e).

(d) Long-term changes in switching schedules

In what way does the switching schedule of a pair change over the period of brood care? Three pairs (6 individuals) were observed for 15, 34 and 35 obs. periods covering egg care (2–3 days) and wriggler care (4–5 days). Data were arranged in three time classes: morning 8.00–12.00 h, afternoon 12.00–16.00 h, evening 16.00–21.00 h. No systematic behavioural recordings were made at night, but casual observations indicate that general activity is very low then, and switching rare.

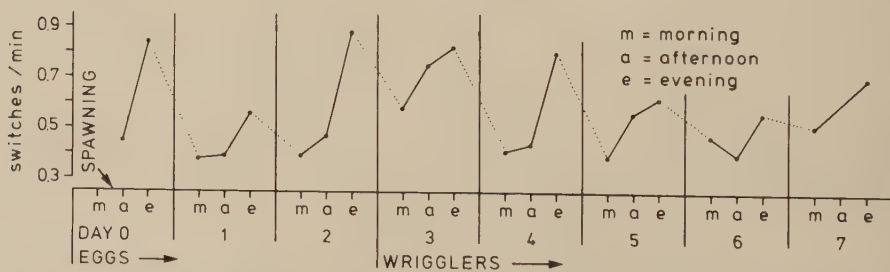


Fig. 8: Median switching frequencies (2–7 values per time class) during egg and wriggler care periods. Dotted lines merely connect observed evening and morning points, and do not represent night switching frequency values

Median values for each time class and day are plotted in Fig. 8. Switching frequency generally increases towards evening. The evening value is always higher than those of the preceding and following mornings. On the other hand, task apportionment, even when corrected for inter-pair differences, showed no recognizable temporal pattern.

Data on more pairs are available for the first and second days after spawning, and narrower time classes can be examined. Data from 121 obs. periods on 10 pairs (18 individuals, 16 breeding cycles) were assigned to 7 time classes consisting of six 2-h periods from 8.00–20.00 h, and a 1-h period 20.00–21.00 h. Fig. 9 gives the median switching frequencies per time class with their interquartile ranges. Despite the variation an increase in switching frequency towards evening on both days is clearly evident. But now a difference also becomes apparent in the days: for each time class the median switching frequency is higher on Day 2.

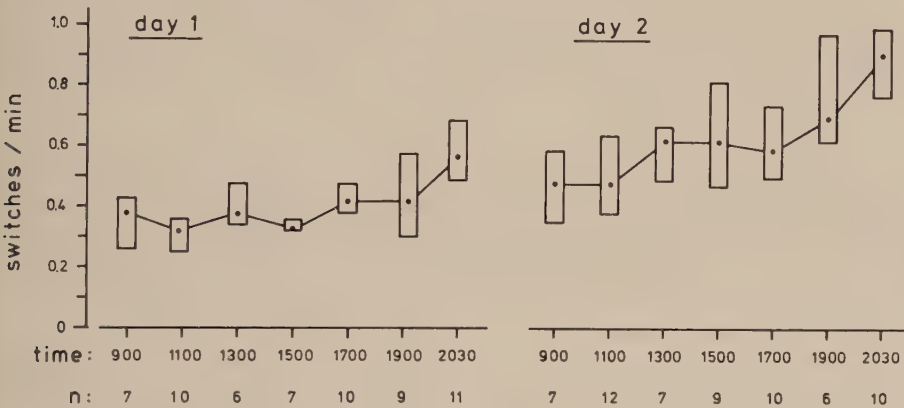


Fig. 9: Median switching frequencies and interquartile ranges for 7 time classes on Days 1 and 2 after spawning

(e) The effect of intruders on switching schedules

Only switching schedules of isolated pairs have been examined so far. But we have already seen in (1) that intruders affect the amount of time parents spend Near the Brood. Do potential brood predators affect task apportionment or switching frequency?

Switching frequencies for 6 pairs (12 individuals) during Days 1 or 2 after spawning were studied with increasing numbers of intruders. As switching frequency had been found to change with the time of day, the values had to be compared with reference values from approximately same-time observations without intruders. Each observed value was therefore divided by the median switching frequency without intruders of its corresponding time class as used in Fig. 9. The resulting quotients are plotted in Fig. 10.

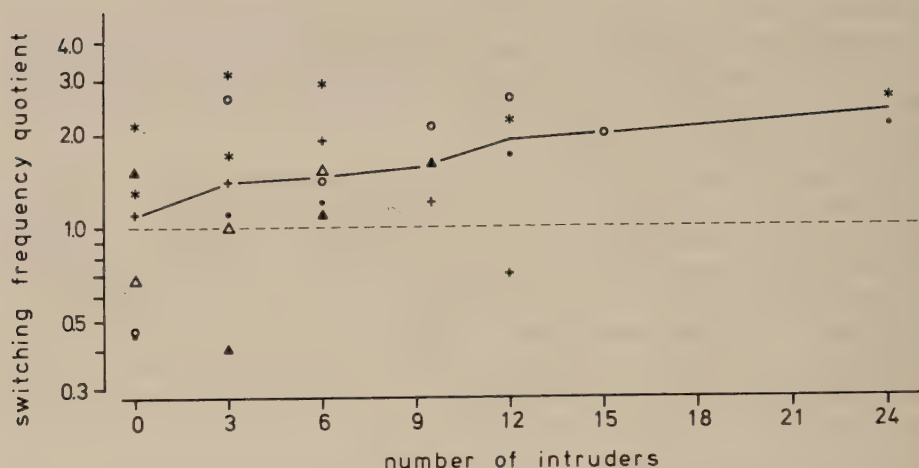


Fig. 10: Switching frequency quotients (frequency *with* intruders divided by the median frequency *without* intruders of the corresponding time class) for 6 pairs (different symbols) with 0—24 intruders. The ordinate scale is logarithmic. Medians of quotient groups are connected

There is a clear tendency for the quotients to lie above 1 for observations with intruders, i.e., for the switching frequency to be higher with than without intruders. A line in Fig. 10 connects the medians of the quotients for groups of observations with the same number of intruders. The positive slope of this line suggests that the effect of intruders increases with their number.

As task apportionment is pair-specific, intruder influence can be ascertained only by comparing the behaviour of the same pair with and without intruders. Sufficient data for this were available for only three pairs. The null hypothesis that task apportionment is unaffected by the presence of intruders could be rejected for these pairs with p values of .094, .110 and .170 (Mann-Whitney U tests). As these three tests have the same null hypothesis their results can be combined (procedure see SOKAL and ROHLF 1969, p. 622), yielding a $p < .05$. This result suggests that intruders do have an effect on task apportionment, although the direction of the change could not be analyzed on the basis of such scant data.

(f) Remarks

Assuming the simplest case, switches could occur whenever the Remote parent happened to pass the brood in the course of rambling about the tank. Such a mechanism of Cichlid brood relief was suggested by LORENZ (1935, p. 344). This would merely determine mean turn lengths, and variation about this mean would be random. But turn lengths vary less than they would randomly (2b), and it must therefore be assumed that a switch becomes increasingly likely with the passage of time since the last one. The parents are in some way measuring time.

Task apportionment and switching frequency varied independently of each other, the one between pairs (2c), the other over time (2d). As switching frequency increased towards evening (Figs. 8 and 9) turn lengths decreased, while the ratio of female to male turn lengths within a pair remained approximately the same. The diurnal variation in switching frequency will be discussed together with the variation of other behaviours in (3e).

The presence of intruders affected both switching frequency and task apportionment (3e). The consequent change in task apportionment corresponds to the change in the relative times spent by the ♂ and ♀ of some pairs Near Brood in the presence of intruders (V, VI) in Fig. 2. The direction of the task apportionment change was not examined further, but the impression during observations was that the parent better able to ward off intruders did most of the defence. This was not necessarily the ♂, as it is in *Aequidens portalegrensis* and *Ae. latifrons* (OHM 1958/59). Nor was it necessarily the larger parent: if intruders offer no direct opposition the greater agility of the smaller mate may be more effective in warding them off.

(3) The Relationship between Position Switches and other Behaviours

So far brood relief behaviour has been treated as just a matter of position change, and tasks have been defined exclusively on the basis of the parents' relative locations. But location is merely a convenient indicator of an animal's behaviour in general. The intermeshing of other behaviours with the switching schedules derived from position changes must now be studied. The following behavioural categories were recorded:

Quiver: A rapid lateral body tremble (performed only in presence of mate).

Chafe Mate: A fish approaches its mate from the rear and glances off its side. (The same movement may be performed off inanimate objects, but not off other conspecifics. Chafing against objects was disregarded in recording the data.)

Charge Mate: A rush at the mate from up to 30 cm distance, also all forms of chasing and biting the mate and mate-directed frontal displays. (Lateral display was not included in the recording.)

Charge Intruder: A rush at a conspecific other than the mate from up to 30 cm distance, also all forms of chasing and biting such intruders and frontal displays directed at them. (Although charges at mate and intruders are basically similar, the former appear very restrained compared with the ferocious attacks on intruders.)

Feed: Any nipping, chewing or sifting mouth motions.

Dig: Gravel is taken up in the mouth and carried for short or longer distances; if any mouth motions occurred, Feed was recorded instead of Dig.

Swim: Any change of location other than those involved in the above categories.

The relationship between positional changes and these behavioural categories is investigated on three levels. Firstly, (a): are there any behaviour changes linked with the observed systematic long-term changes in switching schedules? Secondly, (b): what are the differences in the frequencies of behaviour occurrence in the Proximate and Remote Positions? Thirdly, (c): behaviour distributions *during* such Proximate or Remote turns are shown. In (d) the influence of intruders on these behavioural distributions over turns is considered. (e) draws some conclusions from these results.

(a) Long-term changes in frequencies of occurrence of behaviours

Only two behaviours, Dig and Feed, showed systematic changes during egg and wriggler care periods. For these behaviours the values of δ and η are always summed in the following, as the behaviours of mates showed similar time courses and the values of δ and η per obs. period were correlated with $\tau = .45$ for Dig and $\tau = .31$ for Feed (Kendall rank correlation, $p < .001$ for both behaviours; $n = 87$ obs. periods, treated as independent, on 7 pairs = 14 individuals).

Fig. 11 shows temporal variations of Dig and Feed over the egg and wriggler care periods. Data points are medians from results on three pairs, from the same data as underlie Fig. 8. In Fig. 11 Dig increases towards evening similarly to switching frequency in Fig. 8, but reaches exceptionally high values on the day before and two days after wriggler hatching. Feed takes a contrary course, with high morning and low evening values.

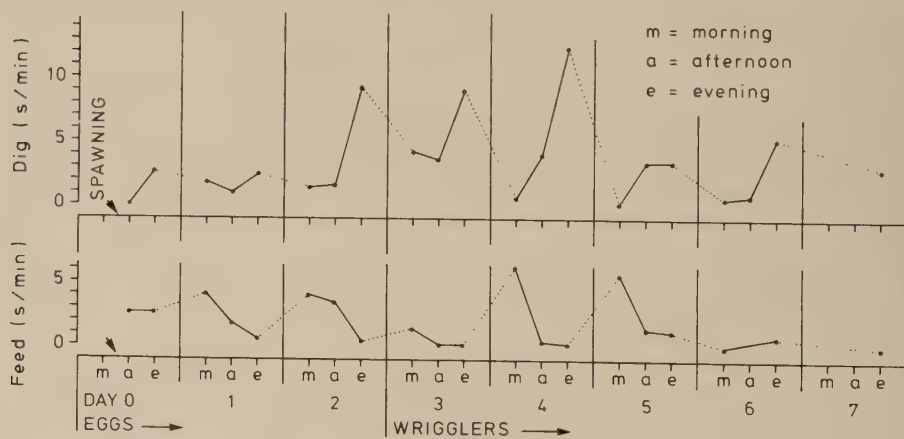


Fig. 11: Median values of Dig and Feed during egg and wriggler care periods from data used in Fig. 8. Dotted connecting lines do not represent actual night values

The correlations between Dig, Feed and switching frequency were examined in data from 7 pairs (14 individuals) taken during egg care ($n = 87$ obs. periods, treated as independent). A significant positive correlation was found between Dig and switching frequency (Kendall rank correlation, $\tau = .30$,

$p < .001$). Feed was significantly negatively correlated with Dig ($r = -.16$, $p < .02$), but its negative correlation with switching frequency was extremely weak ($r = -.06$, $p < .21$).

(b) Behaviour differences between Proximate and Remote Positions

For most behaviours the probability of their occurrence changes radically when an animal switches tasks. Table 1 surveys Proximate and Remote time allocated to various behaviours. Data are from 8 pairs each observed for 1 h in the afternoon of Day 1 after spawning. The medians of each set of 8 values are given. As shown in (3a) the values of Dig and Feed would be slightly different at other times of the day and/or brood care period. However, task-specific and sexual differences discussed below can be regarded as typical for the entire egg and wriggler care periods.

Table 1: Proximate and Remote time allocated to various behaviours

		Near Brood	Charge Mate	Swim	Feed	Dig	Inactive
% of Proximate time	♀	96.8	.2	.4	.0	.0	2.2
	♂	96.3	.3	1.4	.0	.0	2.0
% of Remote time	♀	2.9	.0	24.1	4.2	2.8	58.1
	♂	2.4	.1	27.6	*.6	3.1	64.7
Signif. level of P/R diff.	♀	.01	.05	.01	.01	.01	.01
	♂	.01	.02	.01	.01	.01	.01

* Sexual difference significant at $p < .05$.

For all behaviours listed in Table 1 the differences between behaviour frequencies while Proximate and while Remote were significant for both sexes. Significance levels (Wilcoxon matched pairs test, two-tailed) are given. Most of the Proximate time was spent Near Brood. Both sexes also spent more Proximate than Remote time at Charge Mate (a category including frontal display). Swim, Feed and Dig were performed predominantly while Remote. The members of isolated pairs showed none of the recorded activities for over half the time spent Remote. The only sex-specific behaviour difference was in Feed: ♀♀ spent significantly more of their Remote time feeding than ♂♂ did.

(c) Behaviour distributions over turns

Some behaviours occur at characteristic times of Proximate and Remote turns, or show characteristic changes in frequency during turns. As data from turns of different lengths had to be combined to study these changes, turn lengths were normalized, so that behaviour distributions are described over units which are turn length fractions. The distributions in Figs. 12 to 14 represent several thousand turns per sex from 120 obs. periods on 11 pairs (19 individuals) during egg care. To check that the effects discussed were general, and not distorted by one or two pairs, the behaviour distributions were always scrutinized individually. Only generally valid effects are discussed below.

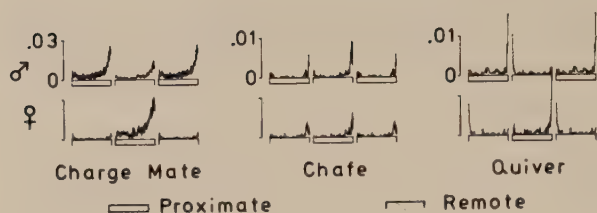


Fig. 12: Distributions of mate-directed behaviours over turns. Ordinate units are fractions of total observation time

Fig. 12 gives the distributions of the mate-directed behaviours Charge Mate, Chafe Mate and Quiver. For each behaviour the distribution is plotted over three successive turns: ♂ Proximate/♀ Remote, ♀ Proximate/♂ Remote, and again ♂ Proximate/♀ Remote. First and last sections of each plot are identical for better comparison of behaviour directly preceding and following switches. Each upper plot gives male behaviour, the lower female behaviour. All turns over 20 s long are combined.

As shown in Fig. 12, both Charge Mate and Chafe tend to occur *before* the mates change positions. Charge Mate occurred more frequently from the Proximate than from the Remote Position (see also Table 1). Quiver occurred both before and after switching, but was performed almost exclusively by the animal ceding the Proximate Position.

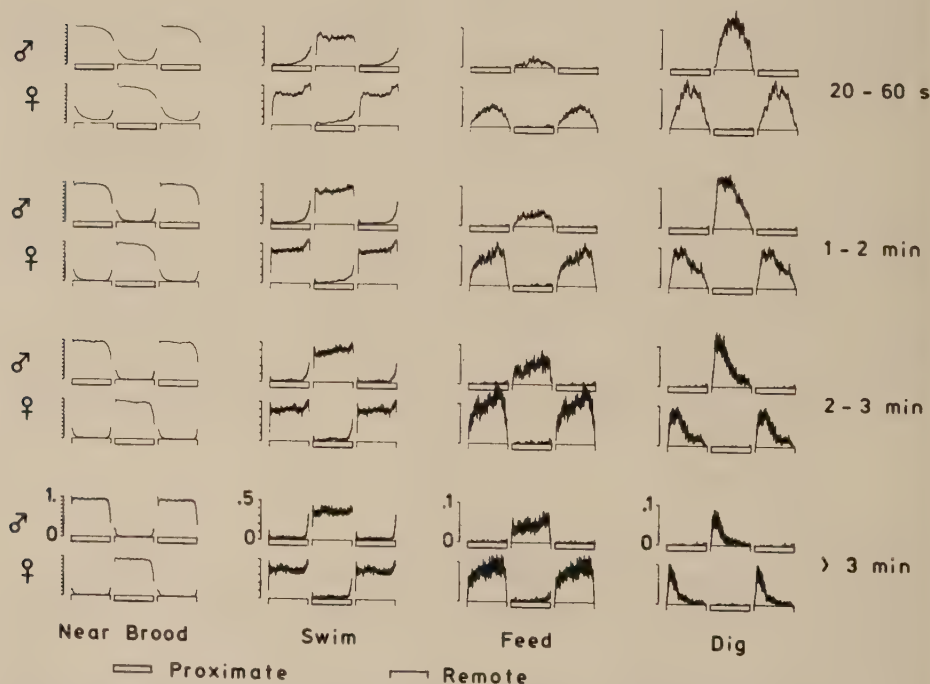


Fig. 13: Distributions over turns for 4 behaviours. Abscissa single line: Remote turn, Abscissa double: Proximate turn. Data arranged in 4 turn length classes. Ordinate units are fractions of total observation time

Fig. 13 shows the distributions over turns for time Near Brood, Swim, Feed, and Dig for several classes of turn length. Near Brood has high values when an animal is Proximate and low ones when it is Remote. An interesting feature is that at the transition from Proximate to Remote the frequency of Near Brood decreases gradually in a sigmoidal curve, whereas it jumps abruptly to its highest values at the reverse transition. This effect was found in all turn length classes. The other behaviours in Fig. 13 occur primarily during Remote turns. Swim is fairly evenly distributed over Remote turns, rising slightly towards the end of both Proximate and Remote turns. No difference in the distribution of Swim is evident in the different classes. Feed increases steadily during Remote turns above 60 s. Dig has the most characteristic distribution; its occurrence is high immediately after a switch into the Remote Position, and then decreases rapidly. In turns of more than 2 min a distinct initial peak of Dig appears, about 80 s long, after which Dig does not increase again.

(d) Behaviour distributions over turns in the presence of intruders

All behaviour distributions so far are for isolated pairs. When confronted with intruders, pairs showing brood defence decreased inactive time, time spent Near Brood (see Fig. 2), and the amounts of Feed and Dig. Mate interactions and Swim showed no appreciable changes.

Are the characteristic distributions of behaviour over turns maintained in these circumstances? Fig. 14 gives distributions of Charge Intruders, time spent Near Brood, Feed and Dig with intruders present (data from 21 obs. periods on 6 pairs). The data have been divided into two classes according to turn lengths; turns of 20–60 s and turns longer than 60 s.

Charge Intruders is performed primarily while Remote, but it also increases steadily during Proximate turns. Time spent Near Brood decreases steadily during Proximate turns, although the gradual change at the transition from Proximate to Remote and the abrupt jump at the reverse transition are still recognizable. For Feed, an increase during Remote turns is no longer evident, but Dig still tends to occur at the beginning of Remote turns longer than 60 s. Both Feed and Dig still occur only during Remote turns.

(e) Remarks

As two animals were observed simultaneously the behaviour categories adopted were necessarily wide; in particular the extensive category 'Near Brood' stands for detailed recording of information on the various brood-directed activities. Nevertheless it is clear that a completely different set of behaviours is performed while Proximate than while Remote (Table 1), and that the change-over from one set to the other is abrupt and coincides well with the mates' change in position relative to the brood (Figs. 12 and 13).

Mate-directed behaviours were all relatively rare, and it is therefore difficult to assess their pertinence to brood relief. Charge Mate was performed mainly from the Proximate Position just prior to switching (Table 1 and Fig. 12). The charged mate did not usually reciprocate in kind but remained

still, presenting its side, with or without fins spread. The Proximate mate seemed able to defer the moment of switching by continued charges, but it was unusual for the Remote mate to precipitate a switch by charging. The distribution of Chafe Mate (Fig. 12) is similar to that of Charge Mate, but this behaviour was often reciprocated, and no difference was found between Proximate and Remote values for chafing. Quiver showed a completely different distribution (Fig. 12), occurring immediately before and after a switch, but only in the parent leaving the Proximate for the Remote Position. It is obviously used in a different context from Charge Mate and Chafe, possibly indicating a willingness to cede the Proximate Position. Quiver is principally a courtship behaviour, and BARLOW (1970) showed it to have appeasement value in *E. maculatus*.

Fig. 2 showed that time spent Near Brood decreases in the presence of intruders; Figs. 13 and 14 show how this comes about. With or without intruders, parents have a high tendency to be Near Brood immediately following a switch. Without intruders this tendency stays high until just before the next switch, when the Proximate parent may swim towards its returning mate (Fig. 13) or show mate-directed behaviour (Fig. 12). But if intruders are present, the tendency to remain Near Brood decreases steadily during a Proximate turn, the parent being increasingly busy charging intruders (Fig. 14).

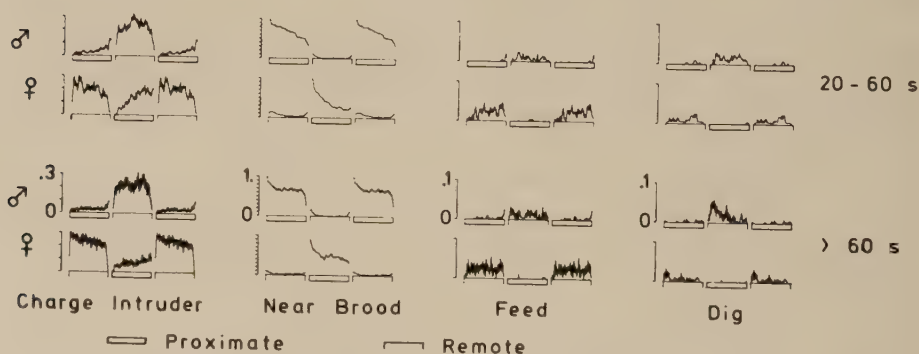


Fig. 14: Distributions over turns for 4 behaviours in the presence of intruders. Data arranged in 2 turn length classes. Ordinate units are fractions of total observation time

Either with or without intruders, Swim, Dig and Feed were performed almost exclusively while Remote. Feed was the only behaviour showing a clear sex-specific difference in frequency of occurrence: ♀♀ spent more time feeding than ♂♂ (Table 1). This is presumably because they have to make up for their greater metabolic investment in the brood. Feed also showed diurnal changes, with higher morning than evening values (Fig. 11). This could possibly be accounted for by the lab feeding schedule (once daily at noon); in the mornings less food was available and the animals were hungry, so that more time was spent foraging.

But the lab feeding schedule can hardly account for the diurnal changes in switching frequency and Dig (Figs. 8 and 11). It would be interesting to

see whether such diurnal rhythms also occur under natural conditions, and if so, how they correlate with environmental factors. The positive correlation between Dig and switching frequency (3a) is elucidated by the peculiar distribution of Dig over Remote turns (Fig. 13): independent of turn length, Dig occurs mainly in one bout immediately after the switch to the Remote Position. The more switches, the more digging bouts occur.

The common causal factor behind digging and switching frequency remains obscure. Investigation of digging behaviour in other Cichlids sometimes showed a connection with attack readiness: HEILIGENBERG (1964, 1965) found that if attack readiness in a Cichlid was increased endogenously or experimentally, digging could increase at the cost of 'sifting' (more or less the equivalent of Feed); readiness to attack could be lowered by the performance of either attacking or digging motions, but not by sifting. Also several authors — BARLOW 1970, LAMPRECHT 1973, REYER 1975 — have seen cause to assume that the sight of the mate elicits attack readiness in monomorphic Cichlids. If these two effects apply for *E. maculatus*, it might be supposed that contact with the mate during switching boosts attack readiness, which is unloaded in a digging bout immediately the Remote Position is attained. The problem is that this idea makes little sense on a functional level. Digging prompted by attack readiness could perhaps be a sensible mechanism if digging were an element of threat behaviour; but not, as is apparently the case in *E. maculatus*, if digging serves exclusively for preparing pits for the wrigglers.

(4) Discussion

The lab results are compared in (a) with what is known of the behaviour of *E. maculatus* in the wild. It is attempted in (b) to form a picture of the decision processes involved in switching behaviour, and the mutual influence of mates during switching. (c) deals with the possible selective advantages of brood relief behaviour.

(a) How 'natural' is the lab behaviour?

Studies on other Cichlids have shown laboratory animals to be sadly underoccupied. Territorial *Haplochromis burtoni* ♂♂ in large laboratory tanks spent 1% of their time interacting with territorial neighbours, compared with 7—32% in the wild (FERNALD 1977; FERNALD and HIRATA 1977). *Lamprologus brichardi* in the lab spent 10% of their time feeding, compared with 80% in the wild (LIMBERGER and TABORSKI, pers. comm.). To what extent is the observed switching behaviour of *E. maculatus* affected by such distorted time budgeting?

Fortunately there is some field information on the behaviour of *E. maculatus*. For animals studied in Sri Lanka, SAMARAKOON (pers. comm.) found switches at intervals of 1—2 min, with each parent spending about 59% of its time tending the brood (fanning and mouthing it and holding station by it) during egg care. About 40% of the time was devoted to wandering and

foraging, about 1% to interactions with conspecifics. After a switch the relieved parent usually foraged. Digging was a relatively rare behaviour (below 1%).

Turn lengths and time spent tending the brood correspond well with lab results. The surprisingly frequent switching in the lab is not an artefact. This conformity is the main argument for judging the observed brood relief behaviour natural enough to warrant functional interpretation.

Field/laboratory differences do exist, however, in the allocation of time to some behaviours. In the lab the time spent on interactions with conspecifics obviously depends on intruder pressure determined by the experimenter. Number and size of the conspecifics used in the intruder experiments drew attacks covering 3–27% of an individual's total time, on the whole well above the average level in nature.

Isolated pairs spent much more time inactive than do wild pairs (Table 1). This was mainly because the animals were fed regularly and food was easy to find, so that relatively little time was spent foraging in the tanks. Curiously, digging took up much more time in the lab than in the wild. On average an isolated pair caring for eggs or wrigglers spent 2–3% of its total time digging. This was certainly not because it needed more time to dig usable pits in the lab; the animals completed up to 15 large pits, of which only 1–4 were used for the wrigglers. This high amount of digging under lab conditions again indicates that a motivational analysis of the digging behaviour of *Etroplus*, and its relation to feeding, could be extremely rewarding (3e).

(b) The decision to switch: when is it made and by whom?

A high degree of interdependency in the behaviour of a ♂ and ♀ cooperating at brood care was shown in (1). The pair members constantly 'agree' to distribute tasks in a certain way, they somehow arrive at a joint decision that determines their separate behaviours. When and how are these decisions made?

Parents change places only when both are in the vicinity of the brood (Fig. 3). Before a switch the patrolling parent returns home. The tending parent has little chance to influence the moment of return, as the mate is usually at a distance and often out of sight. If there is no acoustic switching signal, which is possible but not probable, a tending parent keen to switch would have to leave the brood, find its mate and interact with it. This does not happen, however long the patrolling mate stays away. Sometimes a tending parent makes a charge at the other, but only when it can do so without losing sight of the brood. Even if one parent is removed, the other leaves the brood only for very brief forays or to attack intruders (Fig. 2). The tending mate is not 'free', and therefore has no direct way of reducing turn length; switches must be initiated by the patrolling parent.

What the tending mate could do is *increase* its own turn length — simply by refusing to cede its position. Does this ever happen? There is often a time-lag between the patrolling mate's return and the switch of positions; this is the

period in which the mates interact (Fig. 12). Such delay might be variously interpreted. It could be that some sort of changing-the-guard ritual is involved: if it is critical that the brood is never left without immediate attendance — as the behaviour of single parents suggests — then a mate on the point of switching must make doubly sure that the other really intends to stay, and that no misunderstanding exists. An alternative explanation suggests that the time lag between the patrolling mate's return and the actual switch could stem from conflict of interests between the parents: a switch may be advantageous to the patrolling mate, who initiates it, but disadvantageous to the tending mate, who attempts to delay it. This second is the more likely interpretation, if it is remembered that the smaller mate spends more time than the larger one waiting to attain the Proximate Position — more time Remote but within 15 cm of the brood (2c). BARLOW (1970) has shown that in *E. maculatus* size is generally correlated with aggressive dominance.

The general picture is that turn length is determined primarily by the patrolling mate, although a factor in the timing of its return may well be experience of the other's willingness to cede the Proximate Position. The precise moment of switching is then clinched by both, the larger mate presumably having the last word.

WALLMAN et al. (1979) give a basically similar interpretation of shared incubation in ring doves, suggesting that a stable brood relief pattern 'arises from cooperative interactions between the male and female and that these cooperative interactions are relatively mutual'.

(c) Why take turns? Possible functional reasons for brood relief

A parent should participate in brood care if it is able to contribute substantially to increasing the survival chances of the brood, and its behavioural alternatives to brood care are relatively unrewarding in terms of offspring production (MAYNARD SMITH 1977; GRAFEN and SIBLY 1978). Biparental brood care is therefore promoted if 'the sexes are complementary, either by specialization or by the need for constant attendance at the nest, so that two parents are much better than either parent alone . . .' (GRAFEN and SIBLY 1978).

A need for constant attendance at the nest or brood may well have set the stage for biparental care in substrate-brooding Cichlids, just as in birds. In birds a stationary brood requires thermoregulation, in the Cichlids ventilation. Both services need regular monitoring, they are not storable, and can be administered only on the spot. Presence at the brood may also be a safeguard against raiders in both cases. The brood, then, makes high demands on parental time. In particular, interruptions have a critical length beyond which the odds against brood survival pile up. All things considered, a safe interruption period may be prohibitively short for two reasons: (i) a single parent may not be able to meet its own maintenance needs satisfactorily, and (ii) other important brood care activities may be impeded. Two parents are able to overcome such difficulties simply because they can be in two places at once.

In the first case, if brood attendance conflicts with individual maintenance (i), the obvious solution for cooperating parents is to take turns (save of course for such evolutionary bright ideas as that of the male Hornbill, who carries food to his incubating mate). In birds there is much evidence that the conflicting demands of incubation and foraging account for brood relief behaviour. Comparing various petrel species, for instance, LACK (1968, p. 270) pointed out a dependence of nest shift lengths on food availability. DRENT (1970, p. 16) convincingly demonstrated a relationship between nest relief and foraging schedules in the Herring gull: nest relief schedules depend closely on the foraging rhythm, determined in turn by the tides. In species which are obliged to keep the nest continuously covered, due e.g. to predation, nest desertion by an unrelieved parent is often attributed to its risk of starving. Of the Red-footed booby NELSON (1969) writes: 'The most likely explanation of this desertion is that food shortage caused prolonged absence of the hunting bird and a correspondingly intolerable increase in the mate's incubation stint.' And FISHER (1967) hypothesizes that Laysan albatrosses whose mates did not return stayed on the nest until they reached their 'minimal survival weight'. In general it seems that bird nest relief schedules are substantially influenced by foraging efficiency; an incubating parent needs to be relieved because it must feed, and would desert the nest eventually to do so.

There is no indication of a similar link between brood relief and individual maintenance in Cichlids. It is just not plausible that animals with such a low metabolic rate should be obliged to feed as frequently as every few min. In the lab *E. maculatus*, far from feeding during every patrolling turn, would often ignore food for 30 min or more. Although foraging efficiency is likely to be lower in the wild, this difference cannot account for such perpetual switching, which must waste foraging time, quite apart from the fact that longer turns would allow more efficient search for food. Switching frequency was lower in the lab in fact when much time was spent feeding. And if switching were directed by foraging needs, the ♀'s longer foraging time should have been, but was not, reflected in the task apportionment. On the whole, though the need to forage might explain switching as such, it does not explain the observed schedules.

If not foraging, what does determine the Cichlid switching time-table? Does some other brood care task (ii) interfere with brood attendance? On the face of it such conflict would be no reason for the parents to alternate; the ♂ should, it seems, take on one task and stick to it, the ♀ the other. Switching appears to be a waste of time and energy.

But the picture changes if the two tasks are assumed to carry different cost tags, for instance if a higher risk of predation attaches to a Task A than a Task B. Assuming either parent can perform either task equally well, which should do which?

If two tasks carrying different risks were meted out according to sex, say with all ♀♀ performing the more dangerous Task A, would this task distribution be stable? Other things being equal, fewer ♀♀ would survive, so

that the breeding sex ratio would become biased in favour of ♂♂. Male competition would increase and/or ♀♀ would tend to terminate brood care sooner than ♂♂, as they could find a new mate more readily (GRAFEN and SIBLY 1978). Either effect could lead to task reapportionment; by taking on part of Task A, a ♂ might induce his ♀ to stay on as long as he does. Such a concession might pay him both through increased survival of his present brood and as courtship investment, as the ♀ is more likely to mate with him again if they end this brood care simultaneously, and if she has positive experience of his parental qualities. In effect, parent alternation could be the outcome of a 'bargain' between the parents, each allowing the other a fair share of the cheap brood care task as an inducement to remain on the job. This would assume that each parent is extrapolating from its present to its future task share. Fast alternation could come about as the best possible approximation to simultaneous fair division of the brood care costs, allowing each mate to assess its momentary task load in relation to that borne by its mate. But a limit of brevity is set beyond which switching becomes too frequent for efficient task performance.

Can such a 'fair shares' hypothesis explain the extraordinary brood relief behaviour of *E. maculatus*? For situations of relatively low predation pressure it would appear to be a valid solution. Patrolling would fall into the role of the more costly Task A, as a deserted parent will spend practically its whole time tending. It is conceivable that patrolling brings greater risks to the parent along with greater energy expenditure. This would dovetail with the general impression that the post by the brood is the more desirable one; the larger mate spends more time in this position, and the smaller mate more time 'waiting' for it. If the cost difference between the tasks causes switching, a greater difference should produce more frequent switches. The positive correlation between switching frequency and the amount of digging performed suggests that turns are shorter when energy expenditure during patrolling is high.

The proposition that switching behaviour results from such a compromise sharing of parental tasks rather flags for the situation in which the brood is under acute predation pressure. Here task apportionment changes, switching frequency increases, and during each turn the tending parent becomes increasingly inclined to leave the brood and join the fray. A switch is then no longer necessarily initiated by the Remote animal. It is hard to gauge the pay-off situation in these circumstances. Tasks are presumably no longer complementary, and also a difference in the parents' fighting proficiency may take effect (2 f). Under intense intruder pressure switching can no longer be explained as the result of conflicting individual interests, but could result if the mates maximize their defence efficiency *as a pair*. Possibly switches now occur because the defence efficiency of the Remote parent decreases due to exhaustion, and the rested Proximate animal takes over. But an analysis of the behaviour under intense intruder pressure would require more than laboratory information: how frequent and how intense are attacks in the wild, how many intruders of what size constitute a raiding party, and most important, how effective is the parents' defence?

In most other substrate-brooding Cichlids the sexes are more specialized than in *E. maculatus*; the ♂ of a pair is usually much larger than the ♀, which cannot be paired off experimentally with a smaller ♂. Most of these species also take turns at parental tasks, but most often the ♂ does a larger share of patrolling than the ♀ (BAERENDS and BAERENDS-VAN ROON 1950; BALDACCINI 1973; BAYLIS 1974; KEENLEYSIDE 1978; OHM 1958/59; SMITH-GRAYTON and KEENLEYSIDE 1978). Switches are still too frequent to be explained by foraging needs. But if the unequal task apportionment stems from differing task proficiencies of the sexes, the fair shares idea could be valid here too.

Summary

Etroplus maculatus is a substrate-brooding Cichlid in which mates cooperate at brood care. While one tends eggs or wrigglers the other patrols the territory; every few min they switch tasks. Detailed laboratory observations of this brood relief behaviour were undertaken as a basis for considering its possible evolutionary function.

Section (1) demonstrates the high degree of coordination between the mates. Only one at a time will leave the immediate vicinity of the brood.

(2) examines temporal aspects of brood relief. Parents relieve each other regularly at intervals of 1—2 min. Factors influencing task apportionment to ♂ and ♀ and the frequency of switching are analyzed.

Section (3) investigates the relationship between brood relief and other behaviours.

The Discussion (4) compares the lab behaviour with what is known of the species' behaviour in the wild, examines the decision processes involved in switching behaviour, and suggests possible functional explanations of brood relief in Cichlids compared with birds.

Zusammenfassung

Beim substratbrütenden Cichliden *Etroplus maculatus* beteiligen sich beide Eltern an der Brutpflege. Einer betreut die Eier oder Larven, der andere durchstreift das Territorium; in Abständen von wenigen min tauschen sie die Aufgaben. Genaue Laboruntersuchungen dieser Brutablösung wurden durchgeführt und dienen als Grundlage für Überlegungen über die mögliche evolutive Funktion dieses Verhaltens.

Teil (1) zeigt auf, wie stark die Paarpartner in ihrem Verhalten aufeinander abgestimmt sind. Nur einer auf einmal verläßt die unmittelbare Umgebung der Brut.

(2) untersucht zeitliche Gesetzmäßigkeiten der Brutablösung. Die Eltern lösen einander regelmäßig in Abständen von 1—2 min ab. Es wird untersucht, welche Faktoren die Aufgabenteilung zwischen ♂ und ♀ und die Wechselhäufigkeit beeinflussen.

In Teil (3) werden die Beziehungen zwischen der Brutablösung und anderen Verhaltensweisen betrachtet.

Die Diskussion (4) vergleicht die Laborergebnisse mit Informationen aus dem Freiland, behandelt die Entscheidungsvorgänge bei der Ablösung, und stellt mögliche funktionelle Erklärungen der Brutablösung bei Cichliden und Vögeln vor.

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